DR. GADOW AND MISS ABBOTT ON THE VERTEBRAL COLUMN OF FISHES.

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In the *Publications of the Field Columbian Museum*, vol. 1, pp. 1–54, the writer issued a paper entitled, "On the Structure and Development of the Vertebral Column of Amia." Before this paper appeared, but after it had passed out of my control, there was printed in the *Philosophical Transactions, Royal Society of London*, vol. 186, pp. 163–221, a paper by Dr. Hans Gadow and Miss E. C. Abbott, the title of which is, "On the Evolution of the Vertebral Column of Fishes." This is in many respects an excellent treatise, partly on account of the attempt to define accurately many expressions which have been used rather loosely, and to introduce other terms which are more concise than those hitherto employed. The confirmation of Klaatch's results regarding the manner of development of the vertebral centra of sharks is important, as is also the authors' determination of the origin of the elastica externa. The results of their study of Amia are, of course, of interest to myself, and in some respects they anticipated my own conclusions. On the other hand, the paper is somewhat marred by a number of typographical errors, by the apparent transposition of paragraphs (p. 175), and by rather unsatisfactory text figures. Aside from these minor defects, the work, it seems to me, is pervaded by an erroneous theory concerning the origin of the skeletogenous tissue and the perichordal cartilages.

I will first of all make a remark regarding the definitions of the two kinds of vertebral centers recognized by Dr. Gadow and Miss Abbott. They animadvert on Kölliker's terms "chordal centra" and "perichordal centra"; but the chordal sheath, being a product of the notochord, might not improperly be regarded as a part of the notochord itself; and then Kölliker's names would be appropriate. On the other hand, our authors proceed to say that the centra of the higher Vertebrata,

Kölliker's "perichordal centra," are more properly chordal than are the "chordal centra" themselves; nevertheless, they adopt Kölliker's term in the sense employed by him. If in this connection it is necessary to keep up the distinction between the notochord and its sheath, it would be better to adopt the proposed term, "auto-centra."

One of the most interesting propositions advanced by Gadow and Abbott is that relating to the origin of the skeletogenous tissue. According to them, cells are given off from the ventral portion of the protovertebra, which cells form a pyramidal mass whose base lies against the lower border of the notochord, but whose apex rises to its upper border or higher. It has hitherto been held that all, or nearly all, of the skeletogenous layer has been thus derived. But these authors have discovered another source of skeletogenous cells, and, to judge from the diagrams presented on page 188, at least one-half of these cells originate there. This new fountain of formative materials is found in the upper portion of the protovertebræ. Cells are there emitted which form an inverted pyramid, the apex of which extends to the lower border of the notochord. The dorsal pyramid grows downward in front of the ventral pyramid belonging to the same protovertebra. The bases and the apices of these two sets of pyramids are capable of developing into cartilage, an intermediate zone not attaining this capability. The result is that the bases give rise to the neural and hæmal arches (basidorsals and basiventrals), while the apices give origin to the "intercalated cartilages" (interdorsals and interventrals). From this it will be seen that the two dorsal ridges of the embryo, from which arise the neural arches, are in small part only derived from the lower portion of the protovertebræ while the two ridges below the notochord receive some materials from the upper portion of the protovertebræ.

It may appear remarkable that so great a mass of cells is contributed to the skeletogenous layer by the upper ends of the protovertebral plates without its having been discovered long ago. The production of the dorsal contingent proceeds not earlier than the other, and many observers have witnessed the upward growth of the ventral cells.

Considering too that this discovery is of so much importance, it is unfortunate that the authors did not illustrate their paper with better and more convincing figures. Several text figures representing cross sections are given on page 181; but they are hardly satisfactory. Taking into consideration the curvature of the protovertebral plates it must be exceedingly difficult, in cross sections, to distinguish the limits between two such interdigitating masses of cells. One would suppose that sagittal sections would furnish better evidences, but the authors have not given such a section through the proper portion of the tail.

It has been my fortune to be permitted to examine several well-prepared series of embryos of *Squalus acanthias;* and for this opportunity I am indebted to Dr. W. M. Wheeler, of the University of Chicago. One series consists of sections of a specimen only 5 mm. in length; two other series belonged to embryos 6 and 7 mm. long. I have studied these with the view of testing the statements of the authors referred to, and I trust that I have done this without prejudice. I know no reason for objecting to the theories of the learned authors, in case they are well founded.

In the tail of the 5 mm. *Squalus* cells from the lower border of the protovertebra are seen to be given off toward the notochord. They lie against the latter on each side, and the cluster extends above the notochord so as to reach the lower border of the spinal cord. More anteriorly the skeletogenous cells rise still higher. It was observed that, as the interprotovertebral spaces are approached, the cells appear to drop to a lower level, and may then rise not higher than the middle of the notochord; but this condition lasts for only the thickness of about two sections. It seems to me possible that this may furnish an explanation of some of the appearances presented in the text figures given by the authors on page 181.

In no sections of specimens 5 mm. and 6 mm. long did I find any indications of the emission of cells from the upper ends of the protovertebræ. This was first seen in sections of the embryo 7 mm. long and at about the thirtieth segment behind the head. In this series each body segment comprises

about nine sections. The emission of cells begins at about the fourth section from the front, is seen most distinctly in the sixth, and is not seen in the seventh. Hence, the cells are given off from about the middle third of the upper edge of the protovertebra. A string of these cells can be followed over the spinal cord, where they join those from the other side. They lie above other cells which have come from the ventral border of the protovertebral plate. I have nowhere found any evidences that cells derived from the upper edge of the protovertebral plate grow downward toward the notochord. The sections represented on page 181 of Gadow and Abbott's paper are, in my opinion, in too advanced a stage to reveal clearly the origin of the skeletogenous cells. The evidence of this is to be found in the great number of cells which crowd the space above the spinal cord. These have undoubtedly come from both the ventral and dorsal borders of the protovertebræ. In the sections which I have examined the two sets of cells are caught before they have commingled.

It is to be noted that, according to the authors, all the interdigitating dorsal and ventral masses of cells are formed during the development of the skeletogenous tissue. Also, the colonies of cells are planted which give rise to the interdorsals and the interventrals. Furthermore, each ventral sklerotome fuses with the dorsal sklerotome of the succeeding protovertebra to form a skleromere. But a stage at once ensues in which every trace of segmentation is lost in the sheath of cells surrounding the notochord, and "metamerism is then shown only by the nerves and by the cavities in the dorsal portion of the myotomes." This being true, it would be interesting to learn in what way the fusion of a ventral sklerotome with the dorsal of the next segment differs from its fusion with the dorsal of its own segment.

But the cells which constitute the dorsal and the ventral sklerotomes later give origin to the cartilaginous pieces, eight in number, which are called basalia and interbasalia. How, in view of the fact that in one stage all the boundaries between the sklerotomes disappear, we are to know that the base of the ventral sklerotome is converted into the basiventral cartilage,

and its apex into the interdorsal, we are not told. We can, it seems to me, know this only in case the two structures occupy the same area. But I do not believe that the basiventrals do occupy the same areas that the ventral sklerotomes occupied. It seems to be accepted that the arches, upper and lower (basidorsals and basiventrals), are placed, primitively at least, opposite to or in the septa between the myomeres, while the intercalated cartilages (interdorsals and interventrals) lie opposite the myomeres themselves; but if the views of Gadow and Abbott are correct, the very opposite is true. The basalia would be myomeric; the interbasalia, intermyomeric. (See diagrams on page 188.) The authors hold that the skleromeres alternate with the myomeres, and that the ribs, like the intermuscular septa, are intermyomeric, and they account for this by the peculiar manner of fusion of the sklerotomes; but their explanation assumes the myomeric position of the bases of the skleromeres and their resultant basalia. We have no reason for believing that the neural arch grows out of the upper anterior angle of the skleromere and the rib out of the lower posterior angle.

On the whole, since the materials composing the sheath of skeletogenous cells that surround the notochord do certainly all fuse, so as to be devoid of all segmentation, it is easier to believe that, when differentiation leads to the formation of cartilages, the basalia are constituted out of cells that were derived partly from the protovertebra in front, partly from the one next behind.[1] It is difficult to see why the adjacent edges of two dorsal sklerotomes should not be as likely to remain in permanent fusion as the ventral sklerotome of one protovertebra with the dorsal of another.

In their study of Amia, Dr. Gadow and Miss Abbott have come to conclusions in many ways different from those reached by myself. Indeed, I am obliged to antagonize most of the statements made by these writers. As regards materials, my own appear to be much more complete. So far as I can discover from their paper, they possessed no specimens smaller

[1] We must keep in mind the possibility that the cartilage cells are, or are derived from, immigrants from some outside region.

than 56 mm. in length. At this stage the vertebral column is far advanced in its development.

From the fact that one of the arch-bearing discs of the middle of the tail had united with the archless disc behind it, the authors came to the conclusion that in all parts of the vertebral column the archless discs form the posterior halves of the definitive vertebræ. However, in the unions occasionally formed between the arch-bearing and the archless discs of the tail the one without arches is probably more commonly in front. Besides this, the text of my former paper and its Fig. 10 give proof that the elements of the archless disc belong to the anterior portion of the centrum. This conclusion is confirmed by many other preparations in my possession. Hence, the terms "precentrum" and "postcentrum," employed by Gadow and Abbott, are to be understood in just the opposite sense. If, however, as appears probable, the archless discs in the Stegocephali unite with the arch-bearing disc in front, it would be better to employ terms applicable to both groups. I have been obliged to propose the rather inconvenient terms pleurohæmacentrum and epi-hypocentrum.

Gadow and Abbott also claim to have found, in the trunk region, the lower intercalated cartilages. While admitting the possibility of the correctness of their identification, I am inclined to believe that they are mistaken. What they regard as these cartilages have, in my former paper, been designated as "aortal supports," and appear to be merely extensions downward from the bases of the lower arches. They are, wherever I have seen them, continuous with these arches, except in the hinder dorsal region, where they seem to be cut off from connection with the down-growth of the lower arches by the rapid development of the bone. Somewhat similar developments of the lower cartilages are found in Acipenser for the protection of the aorta, and in this fish the intercalated cartilages also occur. These so-called interventrals do not occur in the anterior portion of the tail of Amia, where we might expect to find them, in case they were such.

It is affirmed by the authors that the upper and lower arches, basidorsals and basiventrals, of the tail of Amia do not lie in

the same transverse plane, but that the basiventrals lie in the plane of the interdorsals. This I regard as a palpable error. Fig. 10 of my paper already referred to was drawn under the camera from a sagittal section near the mid-line. It shows at the right hand that in the middle of the tail the homotype pieces do lie quite accurately in the same transverse plane. Sections of other specimens confirm this view. The authors are correct in their statement that the basidorsals of the trunk region rest on the summits of the interdorsals, but each basidorsal rests on the interdorsal which was originally in front of it, not on the one behind. I can discover no reason whatever for supposing that the basiventrals have been pushed backward.

On page 202 of their paper Gadow and Abbott proceed to explain the arrangement of the arcualia and the manner of their consolidation into the definitive vertebræ. They say there is, outside of the elastica, a thick zone of connective tissue, which forms a layer of bone on its inner suface, and that, in this zone of connective tissue, cartilage cells from the basal portions of the arcualia grow round the chordal sheath preparatory to the formation of the central discs. In the tail, all the arcualia rest on the thin layer of bone which is just outside of the elastica, and are themselves, for the most part, surrounded by bone. In the trunk region, as already stated, the basidorsals are out of contact with the notochord. The outgrowth from the anterior half of the basiventral grows upward in front of the downwardly directed outgrowth from the posterior half of the interdorsal just above it; while the interventral becomes united in a similar way with the basidorsal just above it. These contiguous semi-rings then fuse to produce "complete rings of cartilage, hyaline, and perichondrally ossifying in the arcualia, more fibro-cartilaginous in the newly formed belt." In the tail, of course, there are two such rings for each skleromere. But not all of the outgrowth from each arcuale develops into cartilage, only the anterior half of it. The hinder half becomes connective tissue and then is changed directly into bone. It results from this that there are for each skleromere of the tail two belts of cartilage and

two of bone. The latter develop so cunningly that they unite not the same elements that were united by the cartilage, but the basiventral with the basidorsal of the next myotome behind, and the interventral with the interdorsal of its own myotome.

The scheme of development worked out by the authors is a complex one, and difficult to comprehend; but after having given, I believe, sufficient attention both to it and to a comparison of their statements with actual sections, I feel prepared to make the following remarks.

The cartilaginous arcualia do not rest on any layer of connective-tissue bone. They come into direct contact with the elastica externa and remain in contact with it.

There are from the arcualia no downward and upward outgrowths of cartilage, not even of fibro-cartilage, which meet and fuse to form rings around the notochord outside of any layer of connective-tissue bone. The earliest bone formed starts apparently as a ring around the base of each arcuale where it rests on the elastica. From its place of origin it spreads in all directions. In any section it will be seen rising in one direction against the surface of the cartilage and spreading in other directions over the notochordal sheath. Any outgrowth of cartilage from the arcuale such as described would have to break through this sheath of bone. So far as I can discover, all the bone of the centrum is derived from this earliest stratum by increase in thickness and later by the sending out of anastomosing plates into the surrounding connective tissue. After careful comparison of the figures of the paper of Gadow and Abbott with sections of specimens of various sizes up to 125 mm., I have come to the conclusion that those alleged outgrowths are little, if anything, more than dense masses of connective tissue which occur in the region of the articular ends of the vertebræ. I can discover no cartilage cells outside of the early formed layer of bone. In a specimen 125 mm. long every portion of the original cartilage is yet distinguishable, and I find no trace of such outgrowths or even room for them. We are told that it is the bone belts arising in these outgrowths which bind together the various dorsal and ventral pieces and which constrict

the growth of the chorda. But the arcualia are bound together by the bone which I have described, and it is this bone too which leads to the constriction of the chorda. All this happens before a spicule of other bone is visible.

It might be supposed that the bone which has been described by Gadow and Abbott and that described by myself are identical. I have carefully considered this possibility, but I cannot reconcile their views and my own.

The renewed study of my preparations in the attempt to test the statements of the authors referred to has led to the recognition of some things to which I had attached perhaps too little importance, and which I at one time thought might offer an explanation of the views of those writers. There do exist what appear to be outgrowths from the arcualia, and these outgrowths extend from one arcuale to the other, connecting all of those of each disc; *but these outgrowths lie against the elastica, between it and the first formed bone.* In the anterior dorsal region of a specimen 44 mm. long there is observed such a layer of cartilage, although it may be seen in younger specimens. It is thickest near the articular ends of the centra, while in the intermediate regions it becomes very thin, a single layer of cells. Immediately between the bases of the various arcualia of each vertebral centrum or disc it seems to be wholly wanting, thus producing gaps in what forms practically a sheath of cartilage around the notochord. This reminds us of the sheath of cartilage which surrounds the notochord of the young Lepidosteus, except that in Amia the cartilage is not continuous from one vertebra to those adjoining.

As to the origin of the cartilage, it undoubtedly develops after the layer of bone has been deposited and spreads from the bases of the arcualia. When the bone is first laid down over the elastica it either lies close against this sheath or there are to be seen between the elastica and the bone, a very few nuclei which closely resemble those of the bone-cells already enclosed. A little later the cells lying under the bone increase in number; and gradually they take on the appearance of cartilage cells surrounded by their matrix.

It seems to me that this thin layer of cartilage represents

the tardily developing remains of a more complete sheath of this substance, which must have enveloped the notochord of the ancestors of this interesting fish.

This cartilage is far from occupying the position assigned by Gadow and Abbott to the outgrowths of cartilage described by them, and far from having the thickness of those outgrowths. Nevertheless, in sections taken near the ends of the vertebræ, where, on account of the flaring of the centrum, the cartilage is struck very obliquely, it has the deceptive appearance of being very thick. Furthermore, in such sections, it may have the still deceptive appearance of being mixed up with the dense connective tissue there found. That such sections will explain the figures presented by Gadow and Abbott I am far from affirming; but I can hardly resist the conclusion that the layer of cartilage which I have described has something to do with the outgrowths which they have described and figured.

Figure 1 given on page 204 of their paper presents a familiar appearance, although the notochordal sheath appears unusually thin. The section has evidently been taken near the anterior end of the centrum. The bone there represented belongs to the early formed layer which I have mentioned. Between this bone and the elastica externa is seen a layer of cells which the authors have not referred to. These belong to the layer of cartilage of which I have previously spoken. Below the bone is a collection of cartilage cells marked C. C. and said to belong to the cartilage which surrounds the notochord. It is nothing, however, but the anterior ends of the "aortal supports," the interventrals of Gadow and Abbott. They appear to lie below the bone because the cartilage has grown downward and forward under the first formed layer of bone. In Fig. 2 the supports are still excluded from contact with the notochord for the same reason; but in a section very close behind this the supports would touch the notochord and would at the same time become confluent with the cartilage of the lower arch. That is, neither the cartilage C. C. nor the "supports" *I. V.* are in reality separated by bone from contact with the notochord. The relation of the "supports" to the lower arches is shown in Fig. 9 of my former paper.

In case the outgrowths described by Gadow and Abbott are really present, we should have around the notochord two more or less complete sheaths of cartilage and perhaps two distinct layers of bone.

It seems to me that the essential feature of the theory advocated by Gadow and Abbott, is to be found in their claim that the basidorsals and the basiventrals which unite to produce the definitive vertebra have had their origin from different protovertebræ, and hence correspond to different myomeres. Through the overlap of the myomeres these cartilages are brought into contact and become consolidated. In this way the writers seek to explain the alternation of the myomeres with the skleromeres. But I do not believe that sufficient evidence has been produced to establish this position. An examination of sagittal sections of Amia at various stages of development fails to show that the ventral arches belong to the anterior myomere, the dorsal arches to the posterior myomere. Nor do I find any proofs of any such slant of the intermuscular septa as the authors affirm and represent in their diagrams. The septa take a course across the vertebral centra which is better represented by this figure $\lesssim$, the angle on the right hand being directed backward and placed near the middle of the height of the centra.

Certainly the theory proposed by Dr. Gadow and Miss Abbott is not needed in order to escape the acceptance of the hypothesis of a resegmentation, or "transverse splitting" of the skeletogenous sheath which surrounds the notochord. At a certain stage this sheath has lost all traces of its original segmentation. Why should it regain this segmentation? The cells proceed to differentiation. Some of those lying opposite the intermuscular septa are transformed into the cartilages of the arches. Of the cells opposite the myomeres, some develop into the cartilages which constitute the interbasalia, others into connective tissue which binds the more solid elements together. All this might happen without any transverse splitting and in an organism in which the myomeres do not overlap. The earliest segmentation around the notochord was due to the independent origin of the various sklerotomes; the later segmentation, to differentiation in a mass of similar embryonic cells.